Know thine enemy: Are changes in avian nest attendance predator-specific?

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Abstract

Predation risk is one of the most important factors affecting reproductive success and can significantly influence the behaviour of prey species. Since predation is the main cause of nest failure in birds, it is expected that birds will alter their nest attendance behaviour depending on predation risk so as to make their nests less conspicuous to predators. Birds may also alter the times at which they are active to avoid specific predators. We examined changes in the anti-predator behaviour of breeding song sparrows (*Melospiza melodia*) according to natural and manipulated levels of predation risk. We also determined the key predators of sparrow nests to assess whether birds will alter diurnal activity patterns according to when their main predator is active. Our results suggest that birds are capable of tailoring their anti-predator behaviour according to who their main predator is, and that predator identity is essential to understanding anti-predator behaviour.

Co-Authorship

Dr. Liana Zanette will be given second co-authorship on the manuscript to be published from this thesis. Liana provided valuable advice and guidance in the design of the study, the analysis of the data, and the editing of the manuscript.

Dr. Michael Clinchy will be given third co-authorship on the manuscript to be published from this thesis. He is responsible for designing the camera system used in this study and he provided extensive guidance in the proper use and maintenance of the system. Mike also shared his considerable expertise in designing the study and conducting the fieldwork.

Since this thesis represents a collaboration of work between myself and the co-authors listed above, the pronoun "we" is used where collaborative efforts formed the basis of the matter discussed.

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Chapter 1. General Introduction

Predation risk can greatly affect prey species within ecological time, as it is one of the most important factors limiting reproductive success in birds and mammals (Martin, 1995; Reid *et al*., 1995), and can have significant effects on behaviour (MacLeod *et al*., 2005), physiology (Boonstra *et al*., 1998; Clinchy *et al*., 2004), and offspring survival (Zanette *et al*. 2006). Predation can vary greatly within an animal's lifetime, so flexibility in behaviour related to predation risk will obviously offer fitness benefits above those of fixed traits alone (Lima, 2009).

Predation is the primary cause of nest failure in birds (Nilsson, 1984), and can have a large impact on per capita offspring production at a population scale (Zanette *et al*., 2006). Reducing activity near the nest has been proposed as an anti-predator strategy for small passerines, which reduces conspicuousness and decreases the chance of predators finding the nest (Skutch, 1949; Martin *et al*., 2000b; Ghalambor & Martin, 2002; Eggers *et al*., 2008; Peluc et *al*., 2008). In areas of high predation risk, it is expected that parents would increase this anti-predator behaviour. However, because songbirds remain on their nests at night, regardless of predation risk, anti-predator behaviour will only affect vulnerability to diurnal predators. This suggests that in order for anti-predator behaviour to effectively reduce nest predation rates, the overall predation risk should be high and the primary predators must be diurnal. Therefore, any investigation of factors affecting nest predation should be interpreted with some knowledge of the timing of predation events and thus the relative intensity of diurnal and nocturnal predators. Birds are also able to discern when predation risk is highest and limit their behaviour in order to avoid being active during times of high risk (Krams,

2000; Eggers *et al*., 2005). So in addition to changing behaviour at the nest, birds may alter when they start and end their daily activity depending on when their main predator is active. For these specific behavioural changes to be interpreted correctly, the identity and activity patterns of the common nest predators must be known.

It is important to determine how nesting birds respond to naturally occurring differences in overall predation risk, as well as different primary predators, but the direct manipulation of predation risk would allow researchers to determine if birds can assess a decrease in predation risk and respond by decreasing their anti-predator behaviour. The majority of predator removal studies have focused on the effects of predator removal on nest survival (Cote & Sutherland, 1997; Nordstrom *et al*., 2004; White *et al*., 2008), but few studies have addressed whether parents change their anti-predator behaviour (but see Fontaine & Martin, 2006). It is expected that a decrease in overall predation risk would result in a decrease in anti-predator behaviour, but the types of predators removed should also be important. The removal of diurnal predators should result in a decrease in the anti-predator behaviour of nesting birds, and the removal of crepuscular predators may change when birds start and end their daily activity. So the removal of specific predators, in addition to a decrease in overall risk, should affect changes in anti-predator behaviour.

We used the song sparrow (*Melospiza melodia*) to address questions about level of predation risk, diurnal predation risk, specific predators, and behaviour at the nest. Our study population was divided between areas that differed in overall predation risk (high vs. low), time of predation (diurnal vs. nocturnal), and major predators. From 2004-2008 we recorded behaviour at the nests using video cameras in order to determine whether the behaviour of sparrows at the nest differed according to various aspects of predation risk.

In Chapter 2 of this thesis, we tested three hypotheses regarding parental behaviour, with the goal of determining the relationship between behaviour at the nest and level of predation risk, when predation risk occurs, and specific predators. We measured the anti-predator behaviour of sparrow parents in both high and low risk areas. At the high risk area, predation was primarily during the day. Therefore, if behaviour at the nest was related to predation risk, then birds in the high risk area should exhibit more anti-predator behaviour than those in the low risk area. Within the low risk area, one of the island sites had primarily diurnal predation, while the other two island sites suffered from primarily nocturnal predation. So, if birds only respond to diurnal risk, then sparrows at the diurnal site should show more anti-predator behaviour than those at the nocturnal sites.

The high and low risk areas also had different primary predators, so we tested the hypothesis that birds exposed to crepuscular predators would change the times that they start and end their daily activity. If that was the case, birds at the high risk area, that were subjected to female brown-headed cowbird predation in the morning, should start their daily activity later, while birds at the low risk area, that suffered from evening raccoon predation, should end their daily activity earlier.

We also tested the hypothesis that predator removal, and the resultant decrease in overall predation, would result in a decrease in anti-predator behaviour. However, the types of predators removed should also be important. In 2007 and 2008, we removed specific predators from two of the island sites and measured how behaviour changed post-removal at song sparrow nests. Only the removal of diurnal predators would be expected to result in a decrease in the anti-predator behaviour of nesting birds. The removal of crepuscular predators may change when the parents start and end their day. So the

removal of specific predators, along with a decrease in overall risk, may cause changes in anti-predator behaviour.

The song sparrow is one of the most widespread songbird species in North America, breeding across Canada and the United States, and as far south as central Mexico (Arcese *et al*., 2002). This species is a small passerine, weighing approximately 23 grams, and is characterized by its melodious song, distinctive brown and beige streaked underside, and dark brown spot in the middle of the breast (Arcese *et al*., 2002). Their plumage is sexually monomorphic. Along the Pacific Coast they defend and occupy territories all year round. In other parts of North America they are partially or completely migratory (Arcese *et al*., 2002). They are usually found in forests, shrubs, and marshes, and they forage primarily on the ground, in shrubs, or in the intertidal zone. The diet of the song sparrow is comprised primarily of insects and invertebrates, but they are also known to forage for seeds and fruits when available (Arcese *et al*., 2002).

Male song sparrows establish territories and attract a female, and they defend the territory together for the entirety of the breeding season. Females build open-cup nests, usually in low shrubs or grasses close to the ground, using grass, dry leaves, and other vegetation. The nest-building process takes the female 3 days to complete. Once the nest is built, she lines it with fine grass and hair and then proceeds to lay her eggs. She lays one egg each day until the clutch is complete. Clutches are usually comprised of 2-4 eggs and incubation begins once the penultimate egg is laid. Only the female incubates, and incubation lasts for approximately 13 days. The altricial nestlings hatch asynchronously, usually within 24 hours of each other. They are initially poikilothermic, and the female continues to frequently brood them until they develop endothermy at five days of age. The nestlings are capable of maintaining a constant body temperature eight days after

hatching (Arcese *et al*., 2002). Both parents feed the nestlings, and they typically fledge at 10-12 days of age. Parents continue to feed the fledglings until they are 24-30 days old, after which they are fully independent. A pair can raise up to four successful broods in a single breeding season.

Our study population of song sparrows is located in and around Victoria, British Columbia. The sparrows typically breed from March to August, but are resident year-round. Potential nest predators include snakes, corvids, brown-headed cowbirds (*Molothrus ater*), and small to medium sized mammals (Arcese *et al*., 2002).

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Chapter 2. Know thine enemy: Are changes in avian nest attendance predator-specific?

2.1   Introduction

Predation risk is one of the most important factors limiting reproductive success in birds and mammals (Martin, 1995; Reid *et al*., 1995) and affects individuals in many ways, including feeding (MacLeod *et al*., 2005), activity patterns (Fenton *et al*., 1994; Krams, 2000), physiology (Boonstra *et al*., 1998; Clinchy *et al*., 2004), and offspring survival (Zanette *et al*. 2006). All of these factors in turn can affect an individual's annual reproductive success (Krebs *et al*., 1995; Karels *et al*., 2000; Zanette *et al*., 2006). Predation is the primary cause of nest failure in birds (Ricklefs, 1969; Nilsson, 1984), particularly passerines (Debus, 2006; Zanette *et al.,* 2006; Rodreguez *et al*., 2008), and predation can have a large impact on per capita offspring production at a population scale (Zanette *et al*., 2006).

By reducing activity around nests, small passerines may render their nests less conspicuous to predators, thereby improving nest survival rates and ultimately, annual reproductive success. Decreasing visitation, increasing time spent at the nest, and reducing time away from the nest has been proposed as a strategy for small passerines that reduces the conspicuousness of the nest through reduced activity (Skutch, 1949; Martin *et al*., 2000b; Ghalambor & Martin, 2002; Eggers *et al*., 2008; Peluc *et al*., 2008). It is expected that higher parental visitation rates incur a predation cost, so that individuals with greater activity at the nest suffer higher nest predation. A corollary of this is that reduced visitation rates will be favoured where predation risk is high.

Studies attempting to map the anti-predator behaviour of songbird parents onto nest predation rates at the nestling stage have yielded conflicting results. Some have found that birds exposed to high predation risk do not make fewer visits to the nest (Kleindorfer, 2007), while others have found that birds do decrease nest visitation (Eggers *et al*., 2008; Peluc *et al*., 2008). Spatial and temporal variation in the abundance and type of nest predators (Martin *et al*. 2000a; Schmidt *et al*., 2001; Ghalambor & Martin 2002; Duncan Rastogi *et al*. 2006), and interactions between parental behaviour and those of the predator (Dion *et al*., 2000; Martin *et al*., 2000b; Weidinger, 2002; Muchai & Plessis, 2005) have the potential to account for these conflicting results. Since songbirds sit on their nests all night, decreasing nest activity can only be effective in eluding diurnal visually oriented predators (Duncan Rastogi *et al*., 2006). Thus, we would expect to see a close relationship between nest activity and predation risk in areas where predation risk is highest during the day. By contrast, in prey populations where predators are primarily nocturnal, we would not expect to see large increases in anti-predator behaviour, even if overall predation rates are high. This suggests that the primary predators must be diurnal in order for an increase in anti-predator behaviour to be observed. Therefore, any investigation into factors affecting prey anti-predator behaviour should be interpreted with some knowledge of the behaviour of the dominant predators.

Measuring both overall risk and the time at which most predation occurs is clearly important for the interpretation of the anti-predator behaviour of nesting birds. However, in addition to changing behaviour at the nest, birds may also alter their diurnal schedule according to the activity patterns of their main predator. Birds are able to discern when predation risk is highest and limit their behaviour in order to avoid being active during times of high risk (Krams, 2000; Eggers *et al*., 2005). If different species of predators

have different activity patterns, it is possible that nesting birds may avoid being active when their primary predator is active. For example, studies have shown that if the primary predator is crepuscular, birds become active later in the morning and end their activity earlier in the evening, such that they are not active when their primary predator is active (Krams, 2000). Thus, such specific behavioural changes are related to predation risk, and can also give a hint as to the identity of the primary predators, at least in terms of when the predator is principally active. However, for these specific behavioural changes to be interpreted correctly, the identity and activity patterns of the common nest predators must be known. Unfortunately, the interpretation of nest predation patterns is often limited by the fact that the identities of the primary nest predators in most study systems are unknown (Pietz & Granfors, 2000). The use of camera systems capable of recording at nests has allowed not only the identification of nest predators, but also assessment of the relative importance of predators, their activity patterns, and insight into the behaviour of birds and predators at the nest (Thompson, 2007).

By placing cameras at nests, researchers can determine how nesting birds respond to naturally occurring differences in overall predation risk, as well as different primary predators, across the entire nesting period. However, the direct manipulation of predation risk would allow researchers to determine if birds can assess a decrease in predation risk and respond by decreasing their anti-predator behaviour. Previous studies have often used the presentation of stuffed models to simulate an increase in predation risk (Hatch, 1997; Buhans, 2000; Ghalambor & Martin, 2002; Peluc *et al*., 2008) but this method is limited in that it only shows how birds change their behaviour in response to an immediate risk, and only for a short period of time. A more realistic method of directly manipulating predation risk would be to remove certain predators from the environment.

Several studies have examined how predator removal affects nesting birds, but the results are mixed, with some studies showing an increase in nest survival (Arcese *et al*., 1996; Schmidt *et al*., 2001; Nordstrom *et al*., 2004; Pearse & Ratti, 2004; Fontaine & Martin, 2006; White *et al*., 2008;), while others have found no change in nest survival (Reitsma *et al*., 1990; Kauhala, 2004; Chiron & Julliard, 2006). However, the majority of these studies used artificial nests to determine the effects of predator removal on nest survival, which do not accurately reflect the nest predation rates that birds experience (Zanette, 2002; Moore & Robinson, 2004). It is also possible that the species of predators removed and the relative importance of those predators can help explain differences in the results amongst studies. If secondary predators were removed instead of the primary ones, then there might be little change in nest survival since the primary predators could easily compensate for any decrease in the density of secondary predators (Schmidt *et al*., 2001). Therefore, researchers must determine the importance of various predators in order to establish which should be removed.

The majority of predator removal studies focus only on how predator removal *per se* affects nest survival (Cote & Sutherland, 1997; Nordstrom *et al*., 2004; White *et al*., 2008). Very few studies have addressed whether parents change their anti-predator behaviour in response to predator removal (but see Fontaine & Martin, 2006). It is expected that a decrease in overall predation risk would result in a decrease in anti-predator behaviour, but the species of predators removed should also be important. As argued above, only the removal of diurnal predators should result in a decrease in the anti-predator behaviour of nesting birds, while the removal of crepuscular predators may change when they start and end their day's off-nest activities. So the removal of specific

predators, along with a decrease in overall risk, should affect changes in anti-predator behaviour.

We used the song sparrow (*Melospiza melodia*) to address questions about anti-predator behaviour at the nest and its association with different levels of predation risk and different types of predators. We monitored anti-predator behaviour during the nestling stage using motion-sensitive cameras in order to capture parental nest attendance and predation events. An earlier study (Duncan Rastogi *et al*., 2006) addressed nest attendance and predation risk at the incubation stage in this system, and showed that increased anti-predator behaviour was associated with an increase in nest survival rates, as well as a decrease in diurnal predation events. However, only weak effects were found at the nestling stage in that study, possibly because behaviour was inferred from temperature loggers placed in the nest. Temperature loggers indicate when the female is incubating, so the number of visits per hour, average bout length at the nest, proportion of time spent at the nest, and average bout length off the nest could all be inferred for the female. While such an inference would be reliable for the incubation stage, it would have been inadequate for the nestling stage since both parents feed the nestlings. Also, only a portion of the nestling stage could be studied, since nestlings are able to regulate their own temperature at 5 days of age. In contrast, in the present study, we used cameras to monitor parental behaviour directly. The cameras captured all visits to the nest by both parents across the entire nestling period. Previous studies using camera recordings at the nest have only captured short periods of behaviour, usually no more than a couple of hours long (Fontaine & Martin, 2006). However, it is not clear whether the behaviour during these short periods of recording is representative of behaviour across the entire

day. Our study involves cameras that are capable of recording continuously, so that we are able to capture behaviour throughout the day and across the nesting period.

We used our camera systems to determine the time at which most predation occurred and to identify the principal predators of sparrow nests. Then, we conducted three sets of experiments to assess how predation risk and species of predators affect song sparrow nest activity. The first was a natural experiment where we compared anti-predator behaviour between two areas that differed in overall predation risk, and the time at which most predation events occurred. One area had high predation risk that occurred primarily during the day, while the other area had low predation risk with less frequent daytime predation. We expected song sparrows exposed to high predation risk mainly during the day to show increased anti-predator behaviour, and we used the same four behavioural measures used by Duncan Rastogi *et al*. (2006) to measure this. Specifically, we expected to see a decrease in the number of visits per hour, an increase in the average bout length at the nest, an increase in the proportion of time spent at the nest, and a decrease in the average bout length off the nest. We also determined whether sparrows were sensitive to when their principal predators most frequently attacked nests by identifying the principal predators and then examining when sparrows started and ended their days. Female brown-headed cowbirds (*Molothrus ater*) were the primary predator at the high risk area and were active in the morning (see Results). At the low risk area, the primary predators were raccoons (*Procyon lotor*), which were active in the evening (see Results). Thus, we expected birds to start their days relatively late where cowbirds were of concern and expected sparrows to end their activity relatively early where raccoon predation was prevalent.

However, any behavioural differences found between the high and low risk areas may be confounded by the fact that birds in the high risk area had high predation risk overall, as well as higher diurnal predation. This makes it difficult to discern if differences in behaviour between the two areas are due to overall risk or due to the risk being primarily diurnal. The second experiment was designed to confirm whether diurnal risk *per se* affects anti-predator behaviour, independent of differences in overall risk. To do so, we compared three different sites within the low risk area because each site differed in when predation events mainly occurred, while overall predation rates were similar. We expected to see increases in anti-predator behaviour where diurnal nest predation risk was relatively high. Also, at two of the sites the primary predator was the raccoon, which was active in the evening, while at the third site the primary predators were diurnal crows (*Corvus brachyrhynchos*), which preyed upon nests mainly in the afternoon. Thus, we expected sparrows to end their day relatively early where raccoon predation was prevalent, but expected to see no changes in the time that sparrows started or ended their day where crow predation was of concern.

For the third experiment, we did a direct test to examine the effect that specific predators have on anti-predator behaviour. The primary predators were identified on three different sites within the low risk area and these predators were removed from two of the sites, the third acting as a control. The primary predators were removed, but daily nest survival rates were similar across sites, allowing us to determine if birds responded to changes in when predation mainly occured (i.e., day vs. night). The primary predator at one of the removal sites was nocturnal, while the primary predator at the other removal site was diurnal, so we expected to see changes in the four behavioural variables representing anti-predator behaviour at the diurnal risk site, but no changes in anti-

predator behaviour at the nocturnal risk site or the control site. We also expected to see differences in when the birds started and ended their days between the sites.

2.2   Methods

General field methods

Pairs of breeding song sparrows were monitored in British Columbia, Canada, from 2004-2008. The song sparrow is a multi-brooded species that builds an open-cup nest in low vegetation. A breeding pair is capable of raising up to four broods in a season, ranging in size from one to four young (Arcese *et al*., 2002). Both parents help to feed the young, but only the female incubates and broods. The song sparrow nesting period typically lasts 25 days, with 13 days of incubation and a 10-12 day nestling period.

Sites known to differ in predator pressure (Smith *et al*., 1996; Zanette *et al*., 2003; Zanette *et al*., 2006) were selected. One of the sites had high predator pressure and was located just outside of Victoria on the Vancouver Island 'mainland' (31,284 km2; in the Rithet's Bog Conservation Area), while the other sites had low predator pressure and were situated on several small (<200 ha), coastal islands <2 km offshore (Brackman, Portland, and Russell islands; 123°23'W, 48°35'N). Hereafter, the high predation risk site is known as the "high risk area" and the low predation risk sites are known collectively as "the low risk area". The high risk area supported a greater density of potential predators (Zanette *et al*., 2006; and see Results). There were no significant differences between the high risk area and the low risk area in song sparrow nesting density or in vegetation (Zanette *et al*., 2006).

Nests were found using behavioural cues from the parents. Nests, once found, were checked every 2-4 days and noted as active, fledged, or failed. Each pair's territory was monitored for the entire breeding season.

Video recordings of behaviour

Video data were available for one site at the high risk area and on three different island sites within the low risk area. Each site contained 8-12 breeding pairs. Whenever a nest was found, a small (12 cm long x 2.5 cm wide) camera with infrared diodes was set up at the nest and was connected to a custom-made Digital Video Recorder (DVR) system located up to 250 m away. The system was powered by a series of eight long-cycle marine batteries connected to two solar panels. Each DVR was capable of supporting eight cameras at a time, allowing us to monitor multiple nests at once at each of the sites. The cameras were motion-sensitive and only recorded when there was activity at the nest, which allowed nests to be monitored 24 hours a day for the entire nesting period. The cameras were placed at the nests no earlier than the tenth day of incubation in order to reduce disturbance to the female and decrease the chance of nest abandonment. Two days before camera installation, a "dummy" camera was installed near the nest, which was gradually moved closer to the nest over the following two days. This allowed the parents to habituate to the camera's presence. The real cameras, when installed, were covered with surrounding vegetation in order to obscure them from view from all directions and to prevent predators from using the presence of the camera to help them find nests. We also put up 6-8 dummy cameras at each of the four sites. These dummy cameras were placed in open areas where predators could easily find them to prevent predators from learning to use cameras to find hidden nests. Each nest was

regularly checked using a monitor at the central DVR system so that disturbance at the nest was minimal. The camera recorded at the nest until the nestlings fledged or the nest failed, after which it was removed.

Anti-predator behaviour during the nestling stage was analyzed every second day of the brooding cycle, when the nestlings were 1, 3, 5, 7, and 9 days of age. We recorded four behavioural measurements: the number of times the parents visited the nest per hour; total proportion of time spent at the nest by both parents (daytime activity period); average time spent at the nest by both parents (on bout); and average time the female spent foraging off the nest (off bout). The time that the parents started and ended their daily activity was also recorded, where start time was defined as when the female first departed from the nest in the morning, and end time was defined as when the female settled on the nest to sleep in the evening. If the departure or arrival of the female at the start or end of the day was missed because the motion detector failed to pick up the event, then the mean start or end time was substituted. We confirmed that the data with and without substituted means yielded the same results. Means were calculated for each day of the brooding cycle and for the mainland and islands separately, and were substituted in according to the day and location in which the event was missed. Start and end times were corrected for sunrise and sunset to account for changing daylength across the breeding season by subtracting the start and end time values from the times of sunrise and sunset. The cameras also allowed us to determine the exact fate of the nest, and the fate of each individual nestling. If the nest failed due to predation, the camera provided the identity of the predator, giving us an accurate compilation of the variety of nest predators, the most frequent nest predators and the times of their attacks, and how many nestlings they killed.

Predator removal

To investigate the effects of a direct manipulation of predation risk on song sparrow nest attendance behaviour, we eliminated predation events caused by the primary predators from two of the three island sites. Based on video recordings, the primary predators at the low risk area were the raccoon, the Northwestern crow, and the Western terrestrial garter snake (*Thamnophis elegans*). These predators were responsible for the most attacks recorded by our video cameras (Table 1). A variety of other predators were present within the community but they were responsible for so few attacks that they would have had a minimal effect on nest survival (Table 1). Removal and preventative measures therefore focused on raccoons and crows.

In 2007 and 2008, raccoons were live-trapped on Brackman Island. All removal methods followed national guidelines and were approved by Parks Canada and the Animal Care Committee at the University of Western Ontario. Live-traps were baited with apple slices, sardines, and canned cat food. Three traps were placed at Brackman Island three times over each of the breeding season for approximately a week, and were checked daily. Two raccoons were removed from Brackman Island in each year. Since crows are a native species to the area (unlike the raccoon) we did not remove them from Russell Island. Instead, we made song sparrow nests inaccessible to them using fish netting placed over song sparrow nests. The fish netting had holes that were large enough to allow song sparrows to pass through unhindered, but prevented crows from reaching the nest. Thus, even though the actual predators were not removed, the risk they posed to the sparrow nests was eliminated. No removals or preventative measures were performed at Portland Island, which was used as a control site.

Table 1. Predation events on the eggs and nestlings of the song sparrow (*Melospiza melodia*) by predator species identified by video surveillance of real nests. In the second column the numbers in parentheses indicate the number of attacks by each predator. In the third column the percentages in parentheses indicate the proportion of attacks that occurred during the time frame listed.

Predator	Percentage of Attacks	Time of Most Attacks
Raccoon (*Procyon lotor*)	22% (19)	Evening and Night (79%)
Brown-headed Cowbird (*Molothrus ater*)	21% (18)	Morning (67%)
Northwestern Crow (*Corvus brachyrhynchos*)	18% (16)	Afternoon (75%)
Garter Snake (*Thamnophis elegans*)	15% (13)	Afternoon (85%)
Mink (*Neovison vison*)	8% (7)	Morning (57%)
Domestic Cat (*Felis catus*)	7% (6)	Night (67%)
Mouse (*Peromyscus maniculatus*)	3% (3)	Night (67%)
Rat (*Rattus norvegicus*)	2% (2)	Night (100%)
Barred Owl (*Strix varia*)	2% (2)	Night (100%)
Wasp (*Vespula pensylvanica*)	1% (1)	Afternoon (100%)

Statistical analyses

We calculated daily survival rates for all song sparrow nests found from 2004-2008 following Mayfield (1961, 1975). Nest exposure days at the egg stage were the number of days between when the nest was found and when it hatched or failed. For the nestling stage, nest exposure days were estimated as the number of days between when the nest was found or the eggs hatched, and when it fledged or failed (Mayfield 1975). We summed both egg stage and nestling exposure days for the "both stages combined" calculation. We calculated standard errors following Johnson (1979) and conducted chi-square tests to compare daily nest survival rates using the program CONTRAST 2.0 (Sauer & Williams 1989). Interval survival rates were used to describe the magnitude of difference in nest survival rates between groups and nest stages. Interval survival rates were calculated by raising the daily survival rate to the power of the number of days in the interval (egg stage: 14 days, nestling stage: 11 days, both stages combined: 25 days). Ninety-five percent confidence intervals were calculated for the interval survival rates using methods outlined in Johnson (1979). We tested daily survival rates for 1) presence of cameras (with cameras or without) 2) level of predation risk (high or low) 3) sites within the low risk area (three island sites) and 4) predator removal (before vs. after).

We conducted mixed model ANOVAs to determine significant covariates for each of the behavioural variables. Nest ID was included as a random variable and nestling age as a repeated variable. Many of the behavioural variables (start time, end time, total visits per hour, on bout length at nest, and proportion of time at nest) varied with ordinal date ($F = 4.2$-22.6, $df = 1, 37$-63, $p < 0.001$ - $p = 0.044$) while several others (total visits per hour, on bout length at nest, proportion of time at nest, and female off bout length off nest) varied with brood size ($F = 5.1$-40.3, $df = 1, 42$-66, $p < 0.001$ - $p = 0.028$). We conducted

a regression analysis for each behavioural variable, with data for each day recorded on video as the dependent variable, and the corresponding nestling age, and ordinal date and brood size if they were significant covariates, as the independent variables. For each regression analysis we obtained the residuals for further statistical analyses. We then averaged the residuals across days for each individual nest. Normality could not be achieved for the variable end time, so we conducted a Mann-Whitney U test.

We used a 2x2 contingency table test to determine if sparrow nests at the high and low risk areas differed in the number of predator attacks they suffered during the day vs. night. Then, in order to determine if song sparrow parents exposed to different levels of predation risk showed different anti-predator behaviour, we conducted a forward-stepwise Discriminant Function Analysis (DFA) on the behavioural variable residual averages, with level of predation risk (high vs. low) as the grouping variable. We also conducted one-way ANOVAs on each of the behavioural variables in order to determine which specific behaviours differed between the high and low risk area. To examine whether song sparrow parents exposed to primarily diurnal or nocturnal risk within the low risk area differed in their anti-predator behavioiur, we conducted a forward-stepwise DFA with the time that the greatest predation risk occurred (nocturnal or diurnal) as the grouping variable. Once again, we conducted one-way ANOVAs on each of the behavioural variables in order to determine which specific behaviours differed between the diurnal and nocturnal predation sites.

We tested whether song sparrow parents at sites where predators were removed showed different anti-predator behaviour than parents at a site where no predators were removed. We obtained residuals using the same method as previously described. Some of the behavioural variables (start time, end time) varied with ordinal date (F = 5.0-6.8, df

= 1, 32-46, p = 0.013-0.030) and most of the behavioural variables (start time, end time,

total visits per hour, on bout length at nest, and proportion of time at nest) varied with

brood size (F = 6.3-31.7, df = 1, 36-88, p < 0.001 - p = 0.015). We tested the residual

averages using a forward-stepwise DFA with whether predators were removed or not

(removal vs. control) as the grouping variable. We also conducted one-way ANOVAs on

each of the behavioural variables in order to determine which specific behaviours differed

between the high and low risk area. A 2x2 contingency table test was used to determine

if sparrow nests at the removal and control sites differed in the number of predator attacks

they suffered during the day vs. night post-removal.

The removal of specific predators may have caused different changes in anti-

predator behaviour at each of the three island sites. If the level of daytime risk were

affected at some sites and not others, we would expect to see different changes in the four

behavioural variables that represent anti-predator behaviour post-removal. It is also

possible that the removal of specific predators would cause birds to change when they

start and end their day post-removal. To determine if that was the case, we compared

anti-predator behaviour before and after removal. The six behavioural variables collected

from video recorded before predator removal (2004-2006) were averaged for each day

separately, for each of the three island sites (Brackman Island, Portland Island, and

Russell Island). These averages were then subtracted from the behavioural data recorded

after predator removal had taken place (2007-2008). This gave us a measure of how

behaviour had changed following predator removal. From there, we determined

covariates and obtained residual averages as previously described. Start time ($F_{1,33}$ =

5.908, p = 0.021), and end time ($F_{1,47}$ = 6.4, p = 0.014) varied with ordinal date. Most of

the behavioural variables (start time, end time, total visits per hour, on bout length at nest,

and proportion of time at nest) varied with brood size (F = 6.0-30.6, df = 1, 34-89, p < 0.001 – p = 0.018). We ran the residuals for the six behavioural variables in a forward-stepwise DFA with the island sites (Brackman Island, Portland Island, and Russell Island) as the grouping variable to see whether the three sites would be differentiated into removal and control groups or if they would be differentiated according to which predators were removed. The behavioural data were also analyzed using one-way ANOVAs and Tukey-H post-hoc tests with the three island sites as the independent variable. Whenever the residuals were not normally distributed, we box-cox transformed them to obtain normality. We tested all variables for homogeneity of variance and for normality of error, and applied box-cox transformations whenever necessary. All statistical analyses were performed in SPSS 17.0 (SPSS 17.0 2008) and Statistica 6.1 (StatSoft Inc. 2004). We set α at 0.05.

2.3   Results

A total of 176 song sparrow nests were filmed from 2004-2008 for a total of 1414 days, of which I analyzed 359 nest-days, or 8,616 hours. Nests for which the collected video did not include at least one day of the nestling stage were not included in the analysis. Our database of video recordings of an open cup nesting species is the largest reported thus far in the literature.

Predation events

Eighty-seven predator attacks were captured on video. Predation was the primary cause of total nest failure, with 77% (56 of 73) of failed nests suffering predation. Other

causes such as abandonment (4%, 3 of 73), starvation (9.5%, 7 of 73), and brood

parasitism (9.5%, 7 of 73) made up a relatively smaller percentage of nest failures. The

presence of cameras at the nests did not significantly affect nest survival at the nestling

stage (no camera at nest, 0.52 ± 0.14, camera at nest, 0.49 ± 0.23, $\chi^2 = 0.3$, df = 1, p =

0.59). We could not compare nest survival at the egg stage between camera and non-

camera nests due to the fact that cameras were not installed until the late incubation stage.

Experiment 1

Do song sparrows respond to general predation risk?

As expected, predation rates differed between the high and low risk areas. Nests

at the high risk area were attacked more frequently by predators, with 65% of 48 nests

suffering a predator attack, while only 56% of 128 nests were attacked at the low risk

area. Furthermore, daily nest survival rates differed significantly according to predation

risk (high risk area, 0.93 ± 0.005, low risk area, 0.96 ± 0.004, $\chi^2 = 19.7$, df = 1, p <

0.001), with nest survival being 18% greater when predation risk was low (0.34 ± 0.15)

than high (0.16 ± 0.09). This difference was still significant when the nesting period was

separated into the egg stage (high risk vs. low risk areas, 0.93 ± 0.007 vs. 0.96 ± 0.006, χ^2

= 16.9, df = 1, p < 0.001) and the nestling stage (high risk vs. low risk area, 0.93 ± 0.007

vs. 0.95 ± 0.006, $\chi^2 = 4.8$, df = 1, p = 0.028), with nest survival at the low risk area being

25% greater than the high risk area at the egg stage (low risk area, 0.59 ± 0.21, high risk

area, 0.34 ± 0.14) and 12% greater at the nestling stage (low risk area, 0.59 ± 0.17, high

risk area, 0.47 ± 0.16).

In addition to suffering more nest predation overall, sparrow nests at the high risk area also were attacked more frequently by diurnal predators than nests at the low risk area. We recorded 10 different predator species removing or destroying all or a portion of the contents of sparrow nests from 56 different nests across the four years (Table 1). Of the attacks recorded, 74% (67 of 90) were daytime attacks and 26% (23 of 90) were nighttime attacks. The high risk area suffered significantly more predator attacks during the day (87% of 31 attacks) than the low risk area (68% of 59 attacks; $\chi^2 = 4.0$, df = 1, p = 0.046).

Overall, song sparrow parents at the high risk area increased their anti-predator behaviour. A forward-stepwise DFA showed that anti-predator behaviour was significantly different at the high risk area vs. the low risk area ($\chi^2 = 14.3$, df = 4, p = 0.006). The predictors that best discriminated between the areas were female off bout duration (correlation with canonical root = 0.56), and proportion of time at the nest (correlation with canonical root = 0.51). Song sparrow parents at the high risk area spent less time away from the nest ($F_{1,54} = 5.6$, p = 0.022, Fig. 1c), and spent a greater proportion of time at the nest ($F_{1,54} = 6.0$, p = 0.017, Fig. 1b). Average bout length at the nest ($F_{1,54} = 2.5$, p = 0.12, Fig. 1a) and total visits to the nest per hour ($F_{1,54} = 0.007$, p = 0.93, Fig. 1d) did not differ between the two areas, and did not appear in the model. The discriminant function correctly classified 67% of high risk nests and 90% of low risk nests.
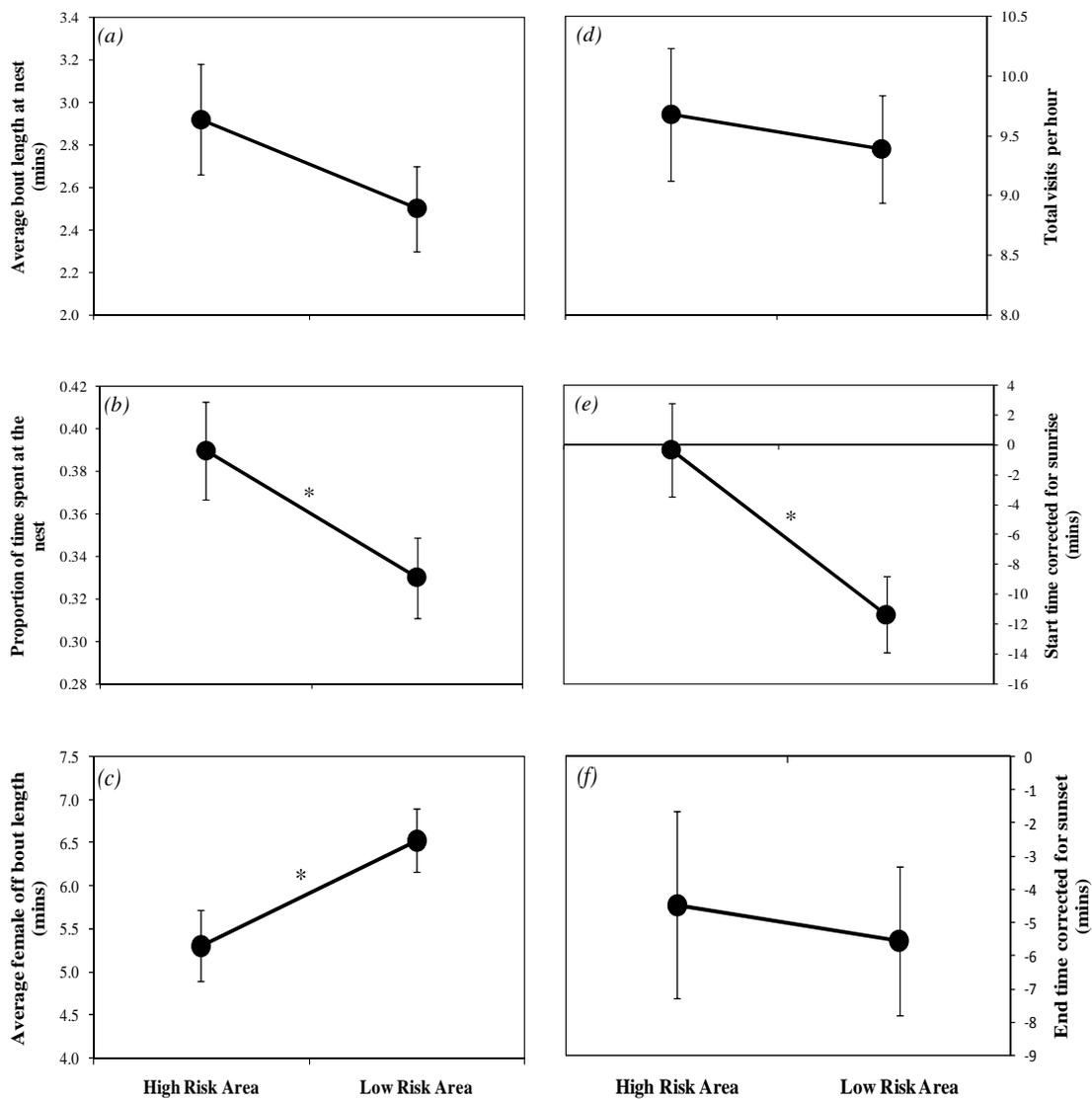
Figure 1. Parental behaviour during the nestling stage at high predation risk and low predation risk areas. Values are least-square means ± SE. Asterisks represent groups that were significantly different according to one-way ANOVAs, * p < 0.05, ** p < 0.001.

High Predation Risk Area

Rat
3%

Raccoon
3%

Cat
19%

BHCO
45%

Snake
10%

Mink
10%

Crow
10%

Low Predation Risk Area

Owl
4%

Mouse
5%

Rat
2%

BHCO
7%

Mink
7%

Raccoon
33%

Crow
24%

Snake
18%
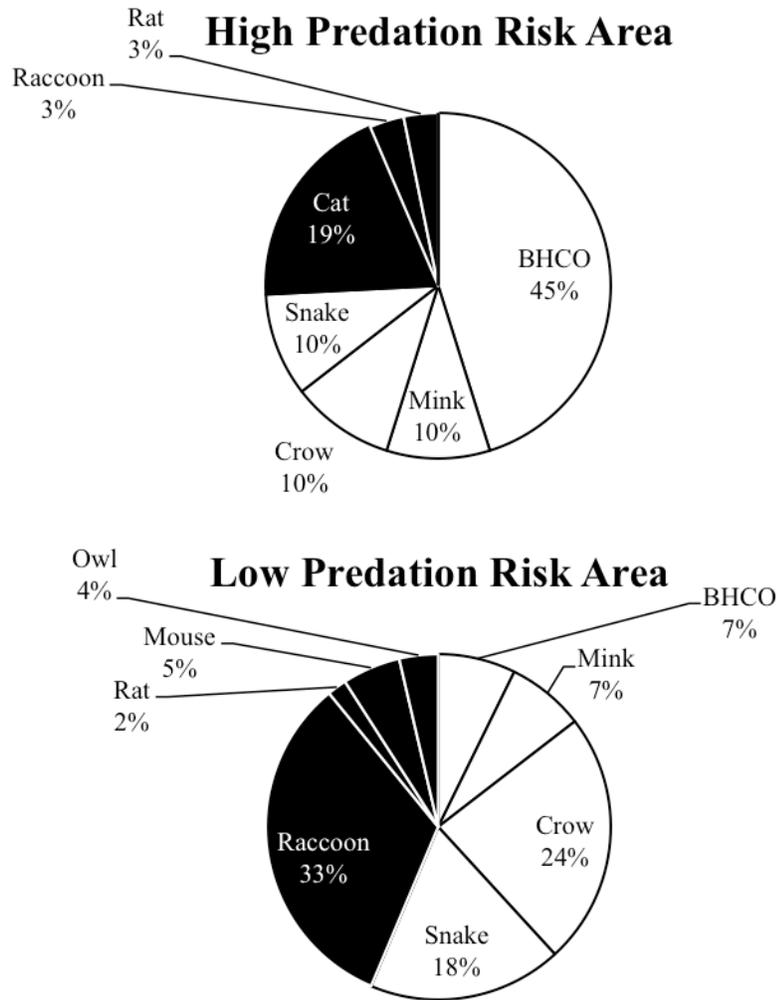
Figure 2. Percentage of diurnal (white) and nocturnal (black) predator attacks at two different areas that differed in overall predation risk. BHCO is an abbreviation for brown-headed cowbird.

Are song sparrows sensitive to different predator species?

The principal predators on sparrow nests differed between the two risk areas. We found that female brown-headed cowbirds were responsible for 45% (14 of 31 events) of attacks on nests at the high risk area while raccoons were responsible for 33% (18 of 59 events) of nest attacks where predation risk was low (Fig. 2). These two predators also had different activity patterns, attacking nests at different times of the day. Cowbirds attacked most sparrow nests during the morning, with 67 % of 18 attacks occurring between 0500 and 1000 h. By contrast, nests at the low risk area were attacked by raccoons most often in the evening and at night, with 79% of 19 attacks occurring between 2100 and 0200 h.

Song sparrow parents appeared to adjust when they started and ended their day in accordance with when their principal predator attacked most often. The DFA (see above) showed that start time was an important predictor in differentiating between the high risk and low risk areas (correlation with canonical root = 0.47). At the high risk area, where female brown-headed cowbirds were the major predators, parents started their day significantly later ($F_{1,54} = 4.39$, p = 0.041, Fig. 1f) than parents at the low risk area. Furthermore, sparrows at the low risk area, where raccoons were prevalent, tended to end their daily activity earlier than those at the high risk area, though the differences were not significant (Z = -1.2, p = 0.23, Fig. 1e), and end time did not appear in the DFA model differentiating the two areas. However, one of the low risk sites (Russell Island) did not have any raccoons at all, the major predator here being the Northwestern crow (see below). Consequently, when we removed that site from our analysis, the song sparrow parents at the low risk area ended their daily activity significantly earlier (high risk area, -

3.32 ± 2.713, low risk area, -7.98 ± 2.583, Z = -2.1, p = 0.037) than parents at the high

risk site.

Experiment 2

Do song sparrows respond to diurnal risk when overall risk is the same?

We examined predation and behaviour within the 3 low risk sites themselves to

further assess whether the differences in anti-predator behaviour observed between the

two risk areas (high vs. low) were due to overall predation risk or specifically to rates of

diurnal nest predation. These three sites allowed us to do so because they had similar

overall predation rates ($\chi^2 = 0.07$, df $= 2$, p $= 0.71$) (Table 2), but varied in when

predators were active (Fig. 3).

We recorded 48 predation events at these three sites (18 at Brackman, 13 at

Portland, 17 at Russell) and found that relatively more attacks were at night (58% of 31

attacks) on Brackman and Portland, while most attacks (93% of 17) occurred during the

day on Russell (Fig. 3). Due to the fact that song sparrows are active only during the day,

we would expect to see more anti-predator behaviour by song sparrows exposed to

primarily diurnal compared with nocturnal predators. This was indeed the case. Anti-

predator behaviour differed between the diurnal vs. nocturnal sites (forward-stepwise

DFA, $\chi^2 = 12.6$, df $= 6$, p $= 0.049$). The predictors that best discriminated between the

sites were total visits per hour (correlation with canonical root $= 0.39$), and average

duration of visits (correlation with canonical root $= 0.37$). Song sparrow parents on

Russell Island made visits of longer duration (Russell, 2.83 ± 0.326, Brackman and

Portland, 2.58 ± 0.259, $F_{1,24} = 4.3$, p $= 0.049$), and tended to make fewer visits to the nest

Table 2. Characteristics of the four sites where sparrow parental behaviour was recorded using a video camera system from 2004-2008. Values are daily survival rates ± s.e.m.

Site	Predation Risk	Primary Predator	Daily Survival Rates	
			Before Removal	After Removal
Mainland	High	Brown-headed Cowbird	0.93 ± 0.005	N/A
Brackman Island	Low	Raccoon	0.94 ± 0.001	0.99 ± 0.005
Portland Island	Low	Raccoon	0.89 ± 0.002	0.98 ± 0.001
Russell Island	Low	Northwestern Crow	0.95 ± 0.001	0.98 ± 0.007

Brackman Island

Crow
19%

Snake
6%

BHCO
13%

Raccoon
62%

Russell Island

Rat
6%

BHCO
12%

Crow
53%

Snake
23%

Mink
6%

Portland Island

Crow
7%

Mink
13%

Snake
7%

Raccoon
40%

Owl
13%

Mouse
20%
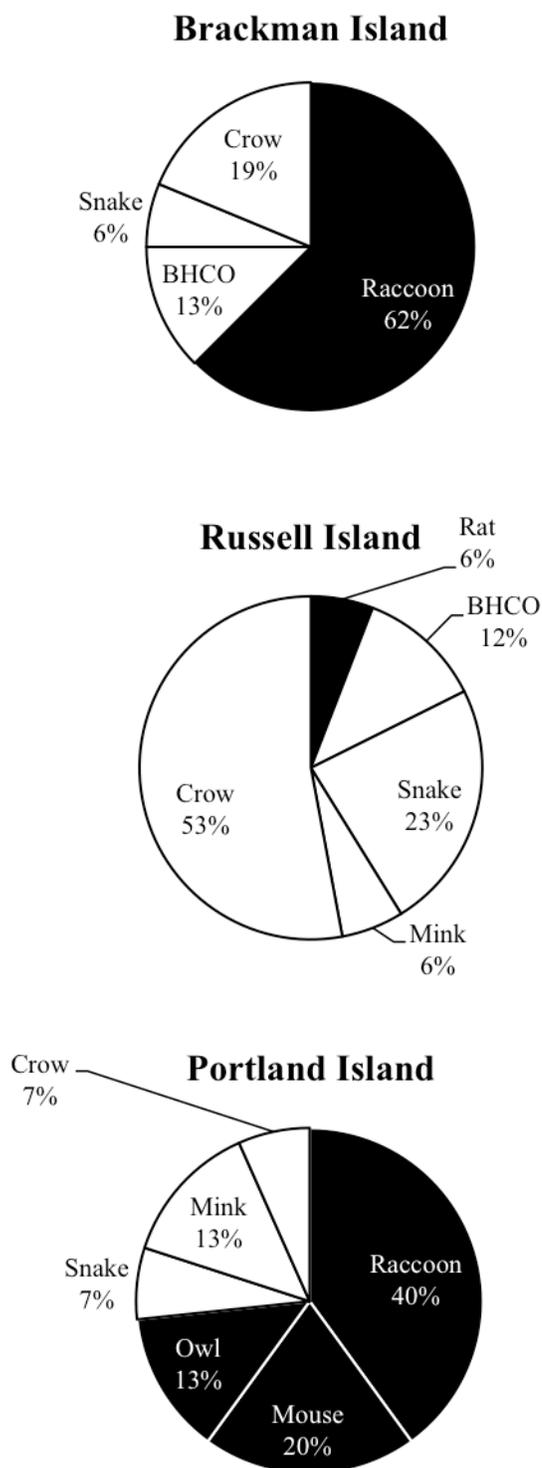
Figure 3. Percentage of diurnal (white) and nocturnal (black) predator attacks at three island sites within the low risk area. BHCO is an abbreviation for brown-headed cowbird.

per hour (Russell, 8.91 ± 0.975, Brackman and Portland, 9.59 ± 0.664, $F_{1,24} = 0.7$, p =

0.42), than parents at Brackman and Portland Islands. Variables that were less important

in differentiating between the two sites were average female off bout length (correlation

with canonical root = 0.19) and proportion of time at the nest (correlation with canonical

root = 0.10; female off bout length: Russell, 6.36 ± 0.702, Brackman and Portland, $7.06 \pm$

0.621, $F_{1,22} = 0.8$, p = 0.40, proportion of time at nest: Russell, 0.32 ± 0.035, Brackman

and Portland, 0.38 ± 0.028, $F_{1,24} = 0.1$, p = 0.76).

Raccoons were the main nighttime predator on Brackman (62 % of 16 attacks)

and Portland (40 % of 15 attacks), and Northwestern crows were the principal daytime

predator on Russell (53% of 17 attacks) (Fig. 3). Consequently, if sparrows respond to

when their primary predator is active, then we should see differences in when the song

sparrows start and end their daily activity. The DFA, which significantly differentiated

the island sites based on anti-predator behaviour, also entered end time into the model

(correlation with canonical root = 0.55). As expected, song sparrow parents on Brackman

and Portland Islands ended their days earlier than parents at Russell Island (Russell, -6.38

± 3.100, Brackman and Portland, -8.54 ± 2.370, $F_{1,24} = 6.5$, p = 0.018). Start time also

entered the model though it only marginally helped to differentiate amongst the island

sites (correlation with canonical root = 0.14) and did not significantly differ between the

island sites (Russell, -8.53 ± 5.586, Brackman and Portland, -15.66 ± 4.209, $F_{1,24} = 0.5$, p

= 0.48).

Experiment 3

Do song sparrows respond to predator removal?

Predator removal significantly increased daily nest survival rates across the nesting period (pre-removal vs. removal, 0.96 ± 0.0042 vs. 0.98 ± 0.0036; $\chi^2 = 11.5$, df $= 1$, $p < 0.001$, Table 2) and at both the egg stage (pre-removal vs. removal, 0.96 ± 0.0058 vs. 0.99 ± 0.0044; $\chi^2 = 9.6$, df $= 1$, $p = 0.002$) and the nestling stage (pre-removal vs. removal, 0.95 ± 0.0060 vs. 0.97 ± 0.0054; $\chi^2 = 4.1$, df $= 1$, $p = 0.043$) separately. However, nest survival also showed an increase at the non-removal site (Table 2), such that there were no differences amongst the three study sites in nest survival rates in the post-removal years (2007-2008, Table 2). This increase in nest survival may be related to the fact that all 3 sites had a greater proportion of diurnal predator attacks post-removal (Brackman Island: pre-removal vs. removal, 19% of 14 attacks vs. 100% of 2 attacks; Portland Island: pre-removal vs. removal, 13% of 8 attacks vs. 43% of 7 attacks; Russell Island: pre-removal vs. removal, 93% of 15 attacks vs. 100% of 2 attack; $\chi^2 = 2.1$, df $= 1$, $p = 0.15$). Anti-predator behaviour also did not vary amongst sites in the removal years (forward-stepwise DFA, Root 1: $\chi^2 = 19.9$, df $= 14$, $p = 0.13$, Root 2: $\chi^2 = 8.9$, df $= 6$, $p = 0.18$).

On Brackman, the major predator that was removed were nocturnal raccoons (Fig. 3), and on Russell they were diurnal crows (Fig. 3). In the removal years, we eliminated predation by raccoons on Brackman (pre-removal vs. removal, 10 vs. 0) and nearly eliminated predation by crows on Russell (pre-removal vs. removal, 8 vs. 1). Furthermore, the number of diurnal vs. nocturnal attacks varied as expected given the specific predators removed. That is, on Brackman Island there was no change in the

number of diurnal attacks, but there was a large decrease in the number of nocturnal attacks (diurnal:nocturnal, pre-removal vs. removal, 4:10 vs. 2:0). On Russell Island there was a large decrease in the number of diurnal attacks, but no change in nocturnal attacks (diurnal:nocturnal, pre-removal vs. removal, 14:1 vs. 2:0). Finally, on Portland Island, there was a slight proportional increase in the number of diurnal attacks with a concomitant decrease in nocturnal attacks (diurnal:nocturnal, pre-removal vs. removal, 1:7 vs. 3:4).

We calculated the change in each behaviour measure in the pre-removal vs. removal years to establish whether predator removal led to changes in anti-predator behaviour amongst the sites. We ran a forward-stepwise DFA using the four behavioural variables that represent anti-predator behaviour during the day. We also included two behaviours (start and end time) that would show if birds responded to the removal of specific predators. Since the predators removed from the sites differed in when they were active (diurnal vs. nocturnal) we expected to see differences in how the birds changed their daytime anti-predator behaviour. In particular, where the primary diurnal predator was removed there should have been a decrease in anti-predator behaviour, and where the nocturnal predator was removed there should have been no change in anti-predator behaviour.

The DFA differentiated the three island sites (Brackman versus Portland versus Russell; $\chi^2 = 53.5$, df $= 12$, p < 0.001). After the removal of the first function, association using the second function was also significant ($\chi^2 = 20.7$, df $= 5$, p < 0.001). The first and second discriminant functions accounted for 62 and 38% of the variation, respectively. Each function mainly separated the site with reduced diurnal predation

(Russell Island) from each of the others. That is, the first discriminant function (root 1) showed the highest discrimination between Russell and Brackman Islands (where the primary nocturnal predator was removed but diurnal predation remained the same) (means of canonical variables; Brackman Island, -1.64, Russell Island, 1.18, Portland Island, 0.69), while the second discriminant function (root 2) separated Russell Island from the control site, Portland Island (means of canonical variables; Brackman Island, 0.18, Russell Island, 0.93, Portland Island, -1.33). The DFA correctly classified 100% of Brackman nests, 73% of Portland nests, and 77% of Russell nests.

The variables that entered the model for root 1 indicated that sparrows at Russell Island decreased their anti-predator behaviour compared with those on Brackman Island, consistent with the idea that prey respond to changes in diurnal risk. Specifically, sparrows on Russell Island reduced both the length of their bouts on the nest (Fig. 4a, correlation with canonical root = 0.46; $F_{2,36} = 6.5$, p = 0.004) and the proportion of time spent at the nest (Fig. 5=4b, correlation with canonical root = 0.34; $F_{2,36} = 4.4$, p = 0.02) while increasing total visits to the nest per hour (Fig. 4d, correlation of canonical root = 0.28; $F_{2,36} = 4.2$, p = 0.023). The control site, Portland Island, did not differ from either Russell or Brackman in any of these measures (Fig. 4a,b,d). Female off bout length also entered into the model for root 1 (correlation with canonical root = 0.21) but we found no significant difference amongst the three sites for this variables (Fig. 4c; $F_{2,35} = 2.6$, p = 0.091).

The times that sparrows started and ended their daily activity were also important in differentiating the two removal sites (root 1). Song sparrow parents on Brackman Island would be expected to end their days later in the years raccoons were removed, and this is what we found (Fig. 4f). End time was an important variable differentiating the
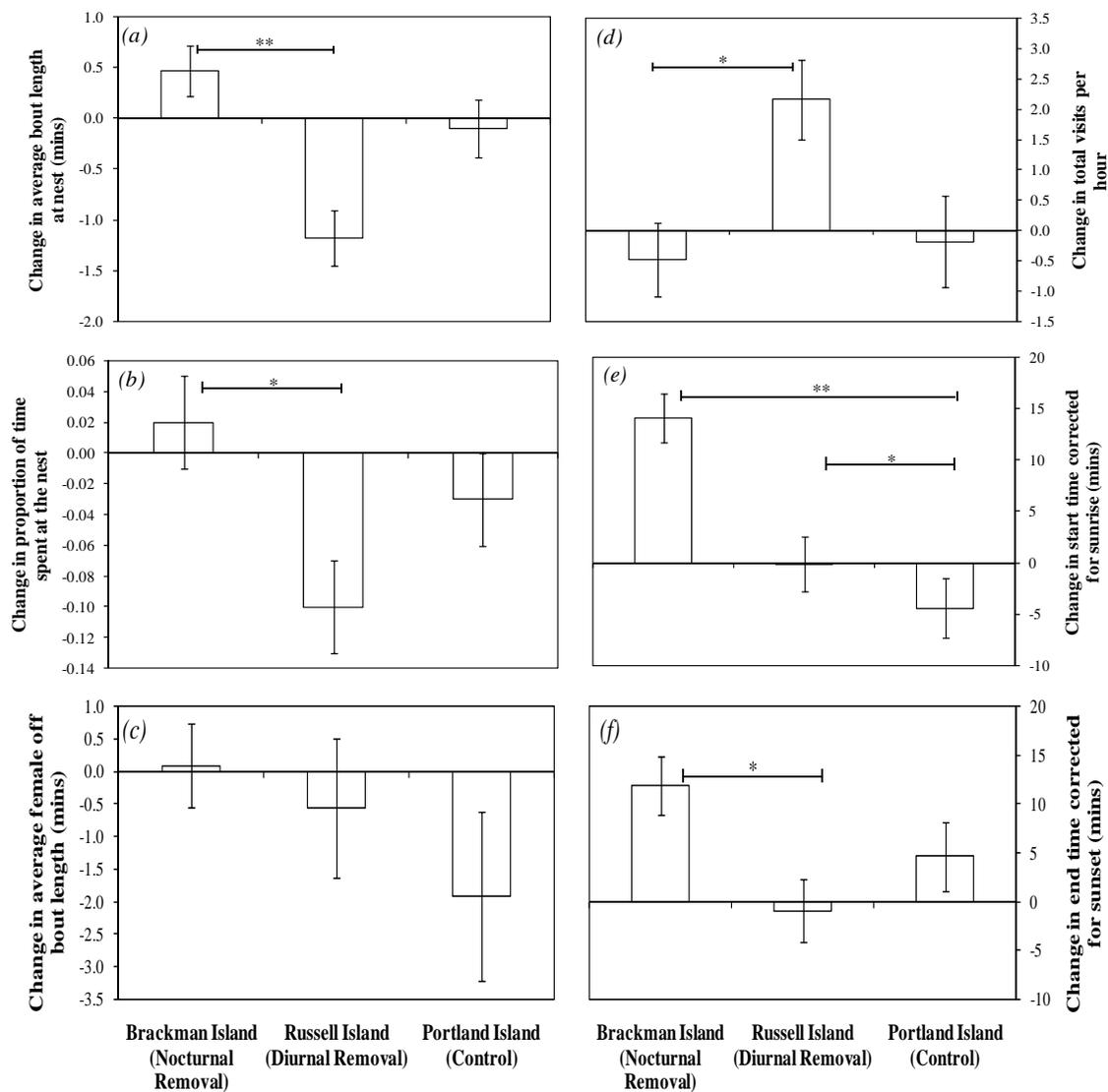
Figure 4. The change in parental behaviour from pre-removal years (2004-2006) to removal years (2007-2008). Values are least-square means ± SE. Lines represent groups that were significantly different according to Tukey post-hoc tests, * p < 0.05, ** p < 0.001.

removal sites from each other (correlation of canonical root = 0.35; $F_{2,36}$ = 4.1, p = 0.026), with sparrows on Brackman Island ending their days later during the removal years. Start time was also an important variable in the model (correlation of canonical root = 0.44). In this case, the removal sites started their days later in the removal years compared to sparrows at Portland Island (Fig. 4e; $F_{2,36}$ = 11.0, p < 0.001).

The variables that best discriminated Russell Island from the control (Portland Island) (root 2) included average duration of visits (correlation with canonical root = 0.31), total visits to the nest per hour (correlation of canonical root = 0.29), average female off bout length (correlation with canonical root = 0.27), proportion of time spent at the nest (correlation with canonical root = 0.22), in addition to start time (correlation with canonical root = 0.56) and end time (correlation of canonical root = 0.12). Again, sparrows on Russell Island decreased their anti-predator behaviour relative to the control (Fig. 4a-c, e-f). Similarly, as with root 1, song sparrow parents at the control site started their days earlier post-removal compared to pre-removal than those at Russell ($F_{2,36}$ = 11.0, p < 0.001, Fig. 4e).

2.4 Discussion

We found through a series of natural and manipulative experiments that song sparrow parents alter their anti-predator behaviour only when the risk of nest predation occurs during the day. In these cases, sparrows increased their anti-predator behaviour by increasing time spent at the nest and decreasing the length of bouts away from the nest, both of which may serve to decrease activity around the nest and make it inconspicuous to diurnal predators. Sparrow parents exposed to primarily nocturnal predation, by contrast, spent less time engaged in anti-predator behaviour. Increasing time spent at the

nest and reducing time away from the nest has been proposed as a form of passive nest defense (Martin *et al*., 2000b) that may reduce the risk of drawing the attention of diurnal visually-oriented predators to the nest (Ghalambor & Martin, 2002; Peluc *et al*., 2008), while also potentially deterring predators if the nest is discovered (Schmidt *et al*., 2001; Weidinger, 2002). In our study, birds in areas with primarily diurnal predation increased behaviour that is consistent with a passive nest defense strategy.

While we expected to see increased anti-predator behaviour by birds exposed to high levels of daytime predation risk, we also found that birds exposed to primarily diurnal predation in an area of low predation risk showed increased anti-predator behaviour. This suggests that, regardless of overall predation risk, sparrows will show increased anti-predator behaviour if predation occurs primarily during the day. Previous studies have addressed the effects of high predation risk on anti-predator behaviour (Ghalambor & Martin, 2002; Eggers *et al*., 2008; Peluc *et al*., 2008), but have not differentiated between diurnal and nocturnal nest predation (but see Duncan Rastogi *et al*., 2006). It is clear that both overall predation risk and the timing of predator attacks must be considered when investigating the anti-predator behaviour of songbird parents.

That sparrows were capable of altering their anti-predator behaviour in accordance to when predators most frequently attack may not be surprising given that birds are sensitive to the activity patterns of particular predators. The idea that birds decrease activity when their predators are active has been investigated in other studies, and it has been found that birds will decrease visitation to the nest during the times that their predators are most active (Egger *et al*., 2008). Our study specifically examined if song sparrow parents changed the times that they started and ended their daily activity in order to avoid morning and/or evening predators. A previous study found that, during the

winter months, birds started to forage later in the morning and ended their foraging earlier in the evening in order to avoid being attacked by crepuscular predators (Krams, 2000). This demonstrates that birds use this strategy in order to ensure their survival. Our study shows that nesting birds will also use this strategy as a means of preventing the loss of their offspring. Our results showed that sparrows exposed to principally early morning cowbird predation started their day later, while birds that experienced high levels of raccoon predation at dusk and at night ended their days earlier. By doing so, the birds may have avoided drawing attention to their nest when their primary predator was active.

Differences in start and end times were also apparent when birds on island sites that differed in diurnal and nocturnal risk were compared. Sparrows at the nocturnal risk sites were subject to high levels of raccoon predation, and thus ended their days earlier than sparrows at the diurnal risk site where the crow was the main predator. Birds that experienced high levels of raccoon predation also started their days earlier than birds exposed to primarily diurnal risk. This may be a result of the sparrows compensating for the time they lost in the evenings. Previous studies have found that birds may increase visits to their nest to feed nestlings during times of low predation risk, in order to make up for a decreased visitation rate when predation risk was high (Eggers *et al*., 2005). Therefore, it is possible that in our study the birds started earlier in the morning, when their primary predator was not active, to make up for ending early in the evenings, when their primary predator was active.

Removing the primary predators from two different island sites had positive effects on song sparrow nest survival rates. We found that, post-removal, daily nest survival rates increased for the removal sites as expected, but we also found that nest survival increased at the control site, despite no removals having taken place there. It is

possible that the predator community at the control site changed naturally between the years, and this change in predator composition affected nest survival rates. Previous studies have found that predator communities can change between years, and that this can in turn affect nest survival (Schmidt *et al.*, 2001; Zanette *et al.*, 2006). Our video data showed that, while the number of predator attacks that occurred at our control site was approximately the same between pre-removal and removal years (number of predator attacks, pre-removal vs. removal, 8 vs. 7) the predators that were responsible for the attacks differed. In the pre-removal years, the majority of attacks were by nocturnal predators (nocturnal vs. diurnal attacks, 7 vs. 1), but in the removal years, the attacks were more equally distributed between nocturnal and diurnal predators (nocturnal vs. diurnal attacks, 4 vs. 3). This increase in diurnal predation may account for the increase in nest survival rates. Birds sit on their nests at night and so their behaviour during the day should have no effect on nocturnal predation. However, as we have previously shown, birds increase anti-predator behaviour when diurnal predation risk is high, which may result in an increase in nest survival. We did not find any behavioural differences among the three sites, despite the apparent increase in diurnal predation at the control site, but this is probably due to the fact that the number of diurnal attacks was fairly equal between all three sites post-removal.

Sparrows show increased anti-predator behaviour when natural levels of daytime predation risk are high, but they are also able to assess changes in predation risk due to the removal of specific predators. In one area we removed predation by the primary predator, the crow, which is a diurnal, visually oriented predator. After the removal, the overall risk during the day was decreased and sparrows showed a decrease in anti-predator behaviour, spending less time at the nest and visiting their nest more frequently.

In the second area, the nocturnal raccoon was the major predator. Diurnal risk did not change after it was removed, and as expected sparrows showed no change in their anti-predator behaviour. Birds in areas where raccoons were removed did, however, end their day later post-removal.

Raccoons attack nests primarily in the evening and at night, and our previous results showed that sparrows ended their day early in areas where the raccoon was the major predator, presumably to avoid being active and drawing attention to their nest when raccoons were most active. After raccoons were removed, the evening was no longer a risky time and the birds remained active later. Sparrows in areas where raccoons were removed also started their days later post-removal. Since the evening was no longer risky and birds were able to end their day later, there was no longer a need for birds to start their day early to compensate for an early end time. This may be why they started their days later post-removal. It was also found that song sparrows at the control site changed when they started their day post-removal, despite no removals being performed there. As previously discussed, the ratio of diurnal to nocturnal predators may have changed naturally between pre-removal and removal years at the control site. This may account for the change in start time.

Our results show that, when the removal of a predator resulted in a decrease in daytime predation risk, there was a resulting decrease in anti-predator behaviour. The only other nest predator removal experiment (Fontaine & Martin, 2006) yielded similar results. It was found that after the removal of a variety of diurnal (red squirrel, *Tamiasciurus hudsonicus*; gray-collared chipmunk, *Tamias cinereicollis*; Stellar's jay, *Cyanocitta stelleri*) and nocturnal (deer mouse, *Peromyscus maniculatus*; white-footed mouse, *Peromyscus leucopus*) nest predators using traps, songbirds increased their

feeding visit rate to the nest. Our results show that the specific predators that are removed are important in predicting how the anti-predator behaviour of nesting birds will change, and suggest that it was the decrease in daytime predation risk that caused the birds to increase their nest visitation rate in the study by Fontaine & Martin (2006).

Predation is the leading cause of nest failure, and thus eluding nest predators should increase annual reproductive success (Zanette et al., 2006). Therefore, when predation risk is high, birds should increase their anti-predator behaviour in order to make their nest inconspicuous to predators. We show a clear relationship between diurnal predation risk and parental behaviour. When exposed to diurnal predation risk, birds exhibited more anti-predator behaviour, and when that risk was removed, they subsequently decreased their anti-predator efforts. The ability to assess changes in predation risk may have benefits in terms of both nestling survival and development. Decreasing feeding visit rate and increasing time spent on the nest, while presumably making the nest less conspicuous to predators, may also result in nestlings receiving less food, which may have negative effects on nestling growth and development. Therefore, it is beneficial for birds to be able to assess whether diurnal predation risk is high or low, and adjust their anti-predator behaviour so that the nest is inconspicuous when risk is high, and nestling feeding is maximized when risk is low. We also conclude that specific predators affect behaviour in different ways. When exposed to morning and evening risk from specific predators, birds responded by starting their days later and ending earlier, respectively. When the evening was no longer risky due to predator removal, they ended their days later. The results of this study clearly demonstrate that the identity and behaviour of predators must be considered in order to fully understand its effects on the behaviour of prey.

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Chapter 3. General Discussion

This study addressed questions regarding the relationship between predation risk and parental behaviour, in particular whether level of predation risk, time of risk, and specific predators affected behaviour. Our study is unique among anti-predator behaviour studies for considering the identity of nest predators and the times at which they attack nests. Not only did we address when predation events occurred, we also used this information to demonstrate that changes in the anti-predator behaviour of sparrows are dependent on diurnal nest predation and the times that their major predators are active.

Our finding that parental behaviour at the nestling stage is not only influenced by high levels of predation risk, but also by specific predators and the time that they attack nests adds considerably to the literature. The majority of work to date has focused on the effects of high predation risk on behaviour (Ghalambor & Martin, 2002; Eggers *et al*., 2008; Peluc *et al*., 2008), while few have considered diurnal and nocturnal nest predation separately (but see Duncan Rastogi *et al*., 2006). Our results show that birds exposed to diurnal nest predation increased time spent at the nest and decreased the length of bouts away from the nest. Birds also showed this increase in anti-predator behaviour when overall predation risk was both high and low. This behaviour may serve to decrease activity around the nest during the day, and as a result, conceal the nest from diurnal predators and/or increase the parents' ability to deter predators. It is clear that the timing of predator attacks is extremely important when investigating the anti-predator behaviour of songbird parents.

To our knowledge, our study is the first to link changes in when birds start and end their day to specific predators, in the context of parental care. Our study specifically

examined if song sparrow parents changed the times that they started and ended their daily activity in order to avoid morning and/or evening predators. We found that in areas where the major predator was most likely to attack nests in the morning, birds started their day later, while in areas where the major predator attacked nests most frequently in the evening, parents ended their day earlier. This demonstrates that nesting birds will also use the strategy of changing start and end times, which may allow them to avoid being active when their major nest predator is active, as a means of preventing the loss of their offspring. Once again, this emphasizes the need for both the identification of nest predators and the times that they attack nests for all studies on nesting bird anti-predator behaviour. Recent advances in video technology are now making it possible to observe birds and predators at the nest, as we did in our study, and nest predator species can now by accurately identified. We anticipate that future research will continue to dramatically expand this area of study.

Our results also showed that birds are capable of responding to experimental manipulations of predation risk. The removal of specific predators caused changes in anti-predator behaviour. Previous studies have focused on how predator removal affects nest survival (Cote & Sutherland, 1997, Nordstrom *et al*., 2004; White *et al*., 2008), while few studies have addressed whether parents change their anti-predator behaviour (but see Fontaine & Martin, 2006). Our results show that predator removal was associated with a decrease in anti-predator behaviour, but only when the removal resulted in a decrease in daytime predation risk. This is consistent with the findings of Fontaine & Martin (2006), who found that parents behave more conspicuously during the nestling stage after a variety of diurnal and nocturnal predators were removed. Our study is the first however, to show that the specific predators that are removed are important in predicting how the

anti-predator behaviour of nesting birds will change. We found that after the removal of raccoons from an area where they were the main predators, birds began to end their day later, presumably in response to the decrease in evening risk. Therefore, researchers must first determine the identity of the main nest predators and when they attack nests. Then using this information they should be able to predict how the removal of certain predators will affect the anti-predator behaviour of nesting birds.

Our results have important implications for future research into the relationship between predation and prey behaviour. In particular, we have shown that it is essential to first determine the identity of the nest predators and their importance in order to answer questions about anti-predator behaviour. Using a video camera system at sparrow nests, we were able to identify a wide variety of nest predator species and the times that they attacked nests. This in turn allowed us to tease out the effects of overall predation risk and diurnal predation risk on anti-predator behaviour, by determining if predation was high in the area, and if it occurred primarily during the day or night. We were also able to assess the effects of specific predators on when birds started and ended their daily activity. We encourage future studies to identify the nest predators in their systems. The importance of predators may vary between geographic areas, as it did in our study, or vary between years, as found in previous studies (Duncan Rastogi *et al*., 2006). We suggest that any investigation of factors affecting nest predation and anti-predator behaviour should be interpreted with some knowledge of the primary predators. Knowing the identity of important predator species will further the understanding of why anti-predator behaviour differs between areas, and may help identify other behaviours, like start and end times, that birds use to avoid specific predators.

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Publications and Presentations

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- monitored song sparrow breeding success: nest searching, handling and banding nestling birds, extracting blood samples
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